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Research Report

A dynamic model for action understanding and goal-directed imitation

Wolfram Erlhagen^{a,*}, Albert Mukovskiy^a, Estela Bicho^b

^aDepartment of Mathematics for Science and Technology, University of Minho, 4800-058 Guimarães, Portugal

^bDepartment of Industrial Electronics, University of Minho, 4800-058 Guimarães, Portugal

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ABSTRACT

The understanding of other individuals' actions is a fundamental cognitive skill for all species living in social groups. Recent neurophysiological evidence suggests that an observer may achieve the understanding by mapping visual information onto his own motor repertoire to reproduce the action effect. However, due to differences in embodiment, environmental constraints or motor skills, this mapping very often cannot be direct. In this paper, we present a dynamic network model which represents in its layers the functionality of neurons in different interconnected brain areas known to be involved in action observation/execution tasks. The model aims at substantiating the idea that action understanding is a continuous process which combines sensory evidence, prior task knowledge and a goal-directed matching of action observation and action execution. The model is tested in variations of an imitation task in which an observer with dissimilar embodiment tries to reproduce the perceived or inferred end-state of a grasping-placing sequence. We also propose and test a biologically plausible learning scheme which allows establishing during practice a goal-directed organization of the distributed network. The modeling results are discussed with respect to recent experimental findings in action observation/execution studies.

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1. Introduction

Humans and other primates are very good in recognizing and understanding goal-directed actions of conspecifics. This cognitive capacity is crucial for any social interaction because it enables the observer to adjust responses accordingly. The advantages of being able to predict consequences of an ongoing action of another individual are obvious in cooperative and competitive situations defining the social life of groups. What are the brain mechanisms underlying the capacity to recognize and understand actions displayed by others? Recent behavioral

and neurophysiological evidence suggests that the neuronal structures involved in action production are to a large extent also activated during action observation. Action understanding might thus be based on a direct matching to the motor commands that an individual may use to reproduce observed actions and their consequences. Rizzolatti and colleagues have forwarded this “direct matching hypothesis” based on their finding of mirror neurons in premotor and parietal areas of monkeys (di Pellegrino et al., 1992; Rizzolatti et al., 1996; for a recent review, see Rizzolatti et al., 2001). Mirror neurons respond either when the animal produces a given action or observes the

* Corresponding author. Fax: +351 253 510401.

E-mail address: wolfram.erlhagen@mct.uminho.pt (W. Erlhagen).

experimenter or another monkey performing a comparable action. Importantly, the actions able to trigger mirror neurons must involve goal-directed behavior such as, for instance, the grasping or placing of an object. Mirror neurons thus seem not to code for the movement per se but for the purpose of the movement. During the past decade, neurophysiological evidence has been accumulated which support the existence of a mirror system matching action observation and action execution also in humans. Moreover, the findings of several brain imaging studies have been taken as evidence that the circuit active during action observation roughly corresponds to the homologous circuit of mirror neurons in the monkeys (Iacoboni et al., 1999; Rizzolatti et al., 2001).

As pointed out by Rizzolatti and colleagues, the suggested functionality of the mirror system provides a natural link between action understanding and imitation. In imitation, the motor description of, for instance, an observed grasping-placing behavior may be turned into an overt action when the response is allowed. Understanding the significance of the action (“placing an object at a new position”) is important since otherwise the reproduced action would represent for the imitator nothing more than a series of meaningless gestures. A lack of understanding limits of course the capacity to apply or adapt the reproduced behavior in a new context.

There are, however, several findings indicating that an explanation of action understanding purely based on a simple and direct resonance phenomenon of the motor system is likely to be incomplete. Humans and also monkeys are able to infer action goals without a full visual description of the action (due to occluding surfaces for instance) by combining partial visual and additional contextual information (e.g., Assad and Maunsell, 1995; Filion et al., 1996; Umiltà et al., 2001). Similarly, it has been shown that infants at the age of 18 month are already able to act on a goal that they had to infer because the demonstrator “accidentally” failed to achieve the end-state of the action (Meltzoff, 1995). Obviously, in both the hidden condition and the error condition, a direct mapping from perception to action is not sufficient to explain the goal-directed behavior of the imitator. Experiments with adults as models and children as imitators challenge in general the direct mapping hypothesis. Very often, a mere copy of the surface behavior displayed by the adult may not be appropriate or may even be impossible due to very different limb and body sizes. Children may nevertheless show their understanding of the task by reproducing the end-state using their own means. In a series of imitation tasks involving hand actions of different complexity, Bekkering and colleagues systematically investigated how the goal of an action (such as touching a dot on a table) affects the mapping from perception to action (Bekkering et al., 2000; Wohlschäger et al., 2003). The fundamental finding was that children primarily focus on reproducing the goal of the action and not on reproducing the means used. However, when the children were explicitly asked to pay attention to how the demonstrator achieved the goal (e.g., left or right hand) they were able to adopt the model’s strategy.

Altogether, these findings suggest that beside the mirror system the neural circuit for action understanding and imitation involves representations, which combine visual cues and contextual information to organize the means needed to achieve an

intentional goal. The prefrontal cortex (PFC) has long been thought to be centrally involved in this process (Pochon et al., 2001; Quintana and Fuster, 1999; for a review, see Miller, 2000). The activity clusters reported in a recent positron emission tomography (PET) study using a goal-directed imitation paradigm fit nicely to this view (Chaminade et al., 2002). In particular, it was shown that the observation and later reproduction of only the means of a known action sequence (i.e., only the grasping but not the placing of a particular object was shown) lead to a strong activation pattern in PFC (see also Buccino et al., 2004). The authors interpret this finding as evidence for a neural processing representing an “automatic” retrieval of the goal underlying the observed action.

Here we present a dynamic model, which aims at substantiating the idea of a distributed neuronal network in which action understanding and goal-directed imitation occur within a continuous dynamic process. In its architecture, the model reflects the basic functionality of neuronal population of distinct but anatomically connected areas in the frontal, temporal and parietal cortex, which are known to be involved in action observation and action execution. Contextual information, action means and action goals are explicitly represented as dynamic activity patterns of local pools of neurons.

Specifically, we apply an imitation paradigm consisting of a grasping-placing sequence to show how the mapping from perception to action may contribute to the inference of the action goal. We also simulate how the knowledge about the action goal can be used to flexibly change between different means to reproduce the witnessed action effect. A second objective of the present modeling study is to illustrate how learning within the network can be exploited for skill growth. Here we focus on changes in environmental constraints and on observed means not in the motor repertoire of the imitator.

To directly illustrate the functionality of the dynamic model, we apply a simulator for a many degrees of freedom robot arm. The model implements a cognitive “decision module” which decides about the means the artifact uses to reproduce the observed or inferred action effect. Since we focus on the goal of the action and do not assume that demonstrator and imitator share the same embodiment, the implementation may be seen as a contribution to solving the correspondence problem that is now considered a major challenge for robot imitation (Alissandrakis et al., 2002; for a detailed discussion, see also Dautenhahn and Nehaniv, 2002).

We proceed as follows: in Section 4, we present the experimental paradigm and the overall model architecture. We also introduce the dynamic model and explain the underlying processing principles. Model predictions for variations of the basic experimental paradigm are described in Section 2. The critical discussion of a number of conceptual implications of our dynamic model is presented in Section 3.

2. Results

2.1. Choice of means and goal inference in an imitation task

In the first simulation example shown in Fig. 1, we illustrate the behavior of the dynamic model for an experiment in which the imitator comes up with its own way of reproducing the

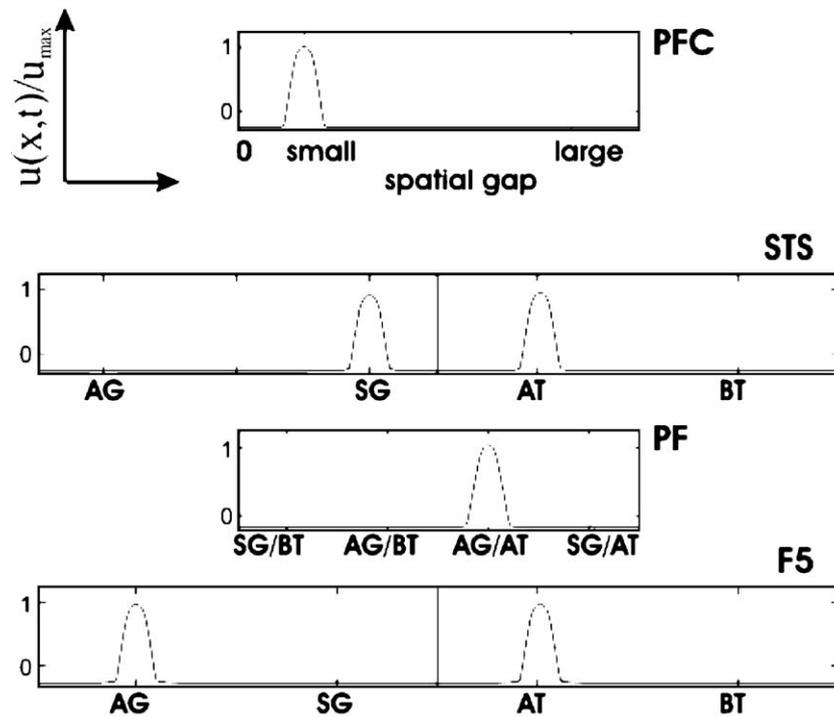


Fig. 1 – The dynamics has relaxed in each network layer to a stable state representing the demonstrated means, the selected goal, the associated action sequence and the corresponding action primitives. The imitator has selected a grip (AG) different to the grip displayed by the demonstrator (SG) to place the object at the higher target.

observed action effect. The demonstrator has placed the object at the higher target combining a grip from the side (SG) and a trajectory above the bridge (AT). In the dynamic model, this information is encoded by localized activation patterns in the goal layer of PFC and in layer STS, respectively. The demonstrated action differs from the imitator’s preferred strategy in the grasping behavior (AG). Since the learned associations to the goal representation dominate the selection process for the sequence in layer PF, the representation of the combination AG/AT becomes suprathreshold. It ultimately suppresses via the inhibitory recurrent connections the SG/AT representation driven by the STS input and simultaneously triggers via the excitatory connections to layer F5 the evolution of the associated motor primitives, AG and AT (compare Supplementary VideoF5 online for a video sequence).

Now imagine that the embodiment of the imitator allows, in principle, to adopt the demonstrator’s strategy to achieve the end-state. This may be the case for instance when the obstacle is sufficiently low. We therefore assume that during training and practice also synaptic links between the particular goal representation and the observed strategy have been learned. The connections are, however, weaker compared to the links to the preferred action sequence. If the imitator is explicitly asked to pay attention to how the demonstrator achieves the goal, the observed means should dominate the decision processes in the mirror circuit. The intentional change in motor behavior can be achieved by weakening the task input to the goal layer. As shown in Fig. 2, a weaker “expectation” about potential targets results in a slower specification of the goal. This in turn also delays the positive input to the associated sequence of means.

As illustrated in Fig. 3, the stable state of the network dynamics now represents a direct matching between action observation and action execution. To illustrate that the decision processes in area F5 directly affect the planning in posture space, we compare in Fig. 4 the overt behavior of the

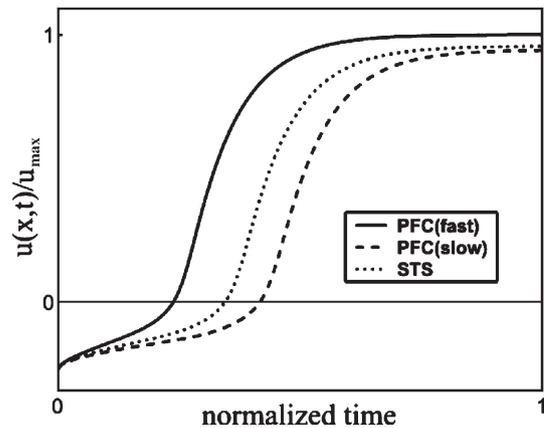


Fig. 2 – Comparison of the time course of the maximum excited neuron in the goal layer of PFC as a function of the relative strength of the task input. With weak preshaping (dashed line), the processing slows down compared to case of strong expectations about possible targets (solid line). The dotted line indicates the typical time course in layer STS. For simplicity, we have chosen for the simulations the identical temporal evolution for the representations of the demonstrated grip and trajectory. The time $t = 0$ represents the onset of the visual stimulation in PFC.

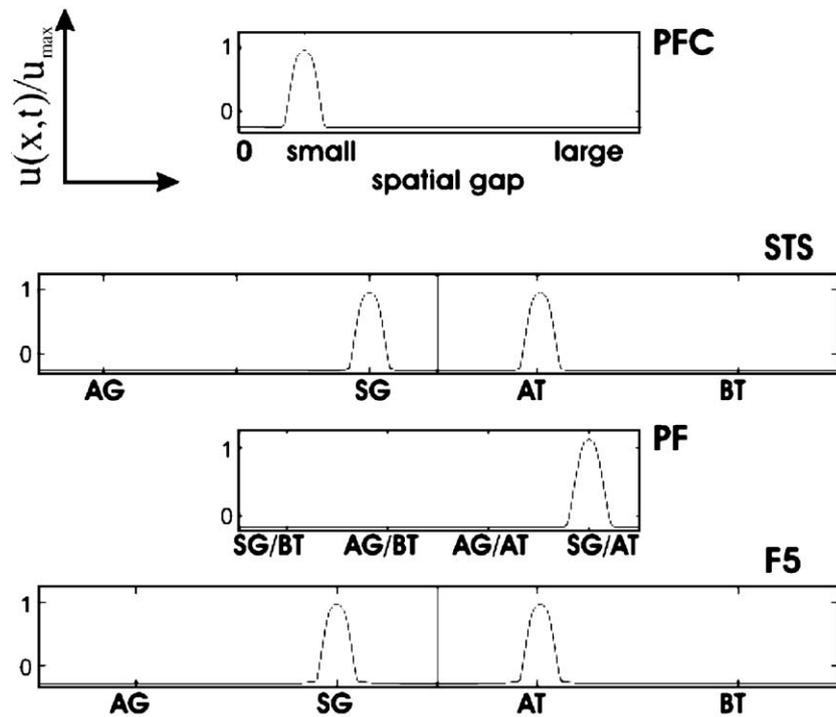


Fig. 3 – Stable states of the network dynamics are shown for the imitation task used in Fig. 1. But now, the imitator was forced to copy also the grip type, SG, displayed by the demonstrator. The adaptation in the response strategy is based on the temporal mechanism illustrated in Fig. 2.

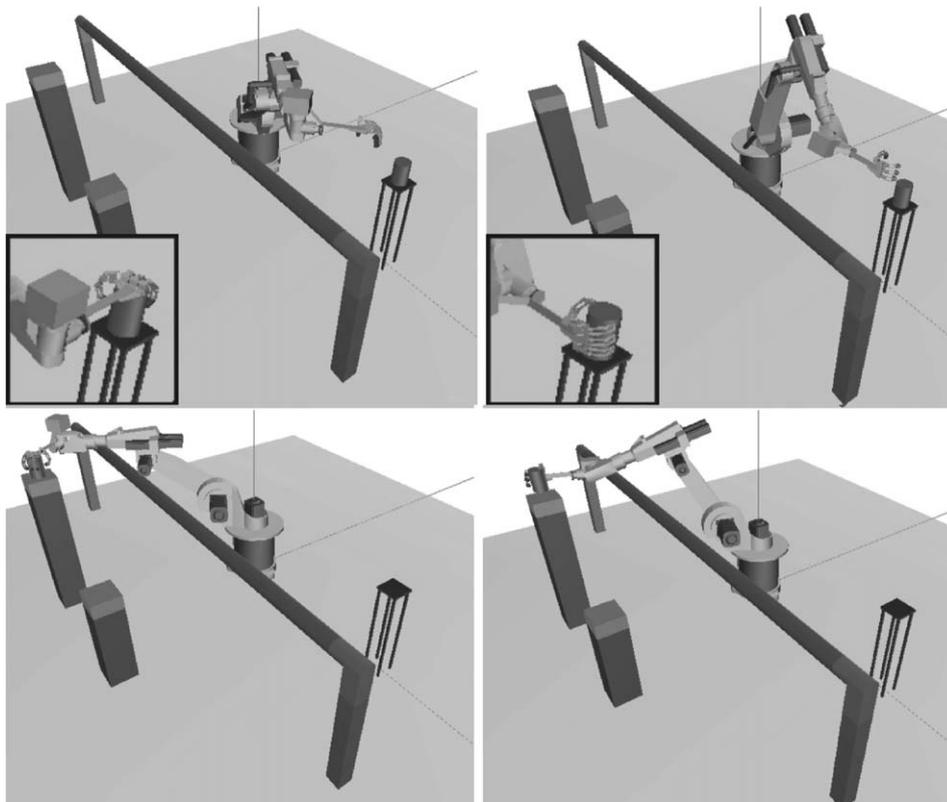


Fig. 4 – The overt behavior of the imitator is shown using a robot simulator. Each column represents two snapshots of postures generated by the path planning system. The column on the left illustrates the imitator's preferred strategy (compare Fig. 5), the column on the right illustrates the case when the imitator made a decision to copy also the grip type displayed by the demonstrator (compare Fig. 7).

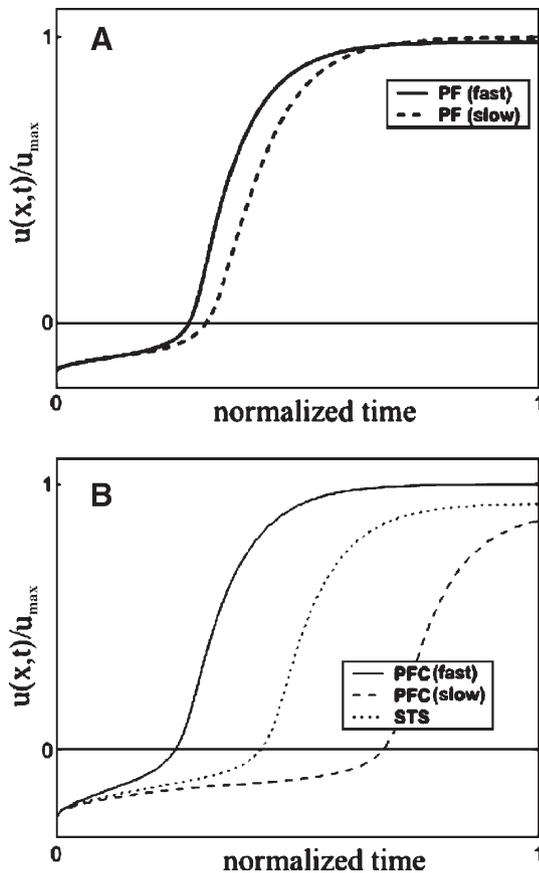


Fig. 5 – The time course of the maximum activated neuron in PF (A) and PFC (B) is shown as a function of the relative strength of the task input. The imitator's means differ from the demonstrated action sequence in both the grip type and the trajectory type. Like in the example shown in Fig. 3, a slowing down of the processing in PFC due to a weaker task input lead in PF to the selection of the demonstrated sequence of means (dashed line). For the faster processing with stronger task input (solid lines), the PF neuron represents the preferred response strategy associated with the perceived goal. To allow for direct comparison, the time course of the representations in STS is plotted in panel B. In both figures, time $t = 0$ represents the onset of the visual stimulation in PFC.

robot arm when the preferred primitives have been selected (left column) with the situation when a direct matching of primitives occurs (right column) (see Supplementary VideoF8l and VideoF8r online for video sequences).

The proposed purely temporal mechanism for adapting the means is not restricted to the first part of the sequence. It works equally well when both the grasping and the transporting behavior have to be adapted. In Fig. 5A, we compare the temporal evolution of the maximum excited PF-neuron for an observed placing at the higher target. With weak preshaping of the goal representations, this neuron represents the demonstrator's sequence SG/BT (dashed line) whereas with strong prior expectation the maximum excited neuron encodes the preferred sequence AG/AT (solid line). In both cases, the evolving pattern in the goal layer represents

the perceived goal (Fig. 5B). For the adaptation case, however, a conflict is introduced since the demonstrated sequence SG/BT represents the observer's preferred strategy associated with the other placing target. The resulting competition between neuronal populations is predicted to further delay the processing in PFC compared to the example shown in Fig. 2.

A second set of simulations shall illustrate the dynamics of the model in an experimental condition in which the goal state is not directly observable and can only be inferred from additional information sources. Recently, Umiltà et al. (2001) have shown that a population of mirror neurons in F5 may encode a goal-directed action also when the crucial part defining that action is hidden from view. The information sufficient to trigger grasping neurons was a hand disappearing behind an occluding surface combined with the knowledge that there is also a graspable object behind that occluder.

The dynamic model offers an explanation of how the integration of partial visual cues, task information and motor knowledge may lead to the inference of the goal. For this purpose, we adapt the occluder paradigm for the bridge task by assuming that only the grasping can be identified and will be represented in layer STS. The visual information about the trajectory and the action goal is missing. The crucial role of the task information is reflected by increasing its relative strength. This constant input brings neuronal populations representing the possible goals and their associated means closer to the threshold necessary to trigger an active response. In Fig. 6, we show snapshots of a model simulation for an inference task in which only the demonstrator's SG-grip was observable (see Supplementary VideoF10 online for a video sequence). The dynamics has relaxed in each model layer to a stable activation peak (solid line). For the preshaped system, the evolving grip representation in STS alone is sufficient to trigger the population in PF encoding the SG/BT sequence. As illustrated by the snapshot of the transient phase of the dynamics (dashed line), this is followed by the evolution of the associated goal representation in PFC. Moreover, due to the reciprocal connections from the frontoparietal circuit to area STS, the model also predicts the evolution of a full visual description of the action including the unobservable trajectory below the bridge. This prediction is in line with findings of a recent fMRI-study using finger movement in an observation/execution task (Iacoboni et al., 2001). The authors report an increased activity in the visual motion area STS also in trials in which the movement was triggered by an abstract, static cue. They interpret this pattern as a reflection of motor-related activity during action execution (but see Keysers and Perrett, 2004 for a different interpretation).

To illustrate the overt imitative behavior in this task, snapshots of the robot arm moving toward the inferred target are shown in Fig. 7. The grasping of the object and the movement trajectory reflect the primitives selected in the action layer F5.

Note that for the inference mechanism to work the grip displayed by the demonstrator must coincide with the grip of the imitator's preferred strategy. Otherwise, we would have to assume the learning of an incongruent mapping from a SG-grip onto an AT-grip (see below).

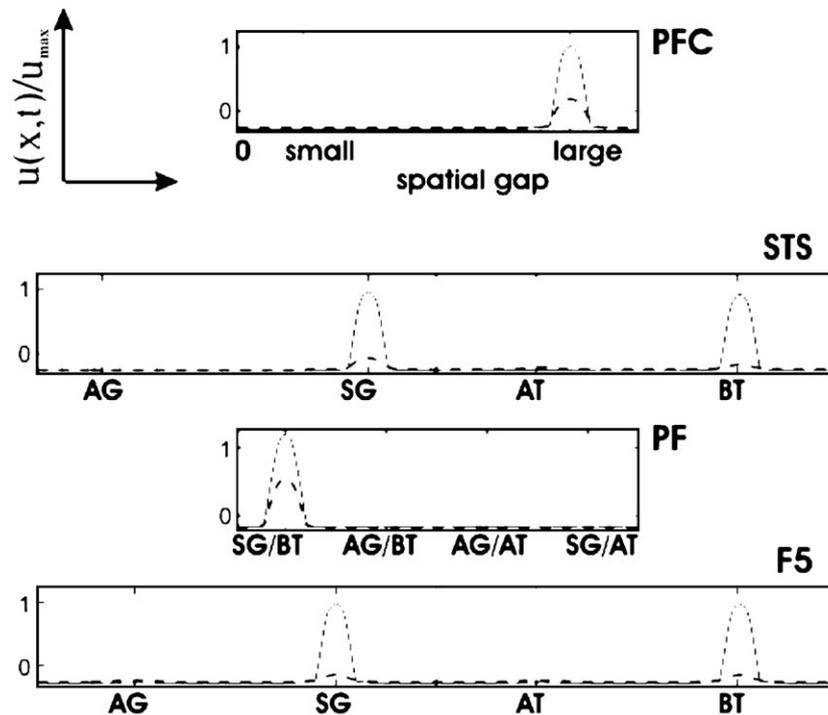


Fig. 6 – Two snapshots of the network dynamics in an inference task are shown. The solid line indicates a relaxed, stable state of the model dynamics whereas the dotted line represents the state of the system in the transient phase. The only visual information available was the grasping behavior, SG, displayed by the demonstrator. The increase of activation in PF (representing the SG/BT sequence) is followed by the evolution of the associated representation of the lower target. The reciprocal connections from PF to STS ensure that finally also the hidden information about the trajectory used by the demonstrator is encoded in the visual area STS.

2.2. Skill growth through correlation based learning

Like other authors before, we suggest that the observation/execution matching system evolves during development through the generalization from a description of self-generated actions to the description of similar actions made by other individuals (Rizzolatti and Luppino, 2001; Oztup and Arbib, 2002; Keysers and Perrett, 2004). Thus, in a first learning phase, the repeated observation of our own hand action is assumed to establish a link between motor primitives and the high-level visual descriptions. Because of the perfect synchrony between action observation and action execution, the learned associations will represent a congruent mapping. This congruency naturally becomes broader when the mapping is also applied to goal-directed actions of others. For instance, the other individual might use a different grip type or even another effector when grasping an object. This difference in the means should of course not disturb the understanding of classes of mirror neurons with a broader congruency, independent of effector or grip type (Rizzolatti et al., 2001), may be seen as experimental evidence supporting the existence of an abstract, goal-directed matching mechanism.

Even more direct evidence comes from a recent study by Fogassi and colleagues (Ferrari et al., 2005) in which grasping neurons in F5 were described which fired when the monkey observed actions performed with a tool. Given the potential role of these “tool-responding mirror neurons” in understanding actions not strictly in the motor repertoire of the observer,

the question is how such high-level motor representations may evolve during development and practice. The following model simulation shall illustrate under which experimental conditions a biologically plausible Hebbian learning rule may establish the abstract mirror properties. Concretely, we suppose that the demonstrator uses a tool unknown to the observer to first grasp and then place the object at one of the goals in the Bridge paradigm.

The first condition for learning the mirror properties is that repeatedly witnessing the tool-use leads to a new classification of the action in terms of the type of grasping. The trajectory, on the other hand, may still be categorized as either above or below the bridge. A detailed description of methods for classifying hand motion goes beyond the scope of this article. Several learning algorithms which exploit statistical regularities have been proposed over the last couple of years (for a recent review, see Ritscher et al., 2003). In the model, we simply assume that a subpopulation of neurons in layer STS specifically encodes through a self-stabilized activity pattern the new grip type “IG”. Using excitatory neurons with Hebbian plasticity, Amit and Brunel (1997) have shown that the structured neuronal connectivity necessary to guarantee for the coexistence of a persistent local activation pattern and a stable resting state may develop during stimulus learning.

The second condition for learning the abstract mirror properties is that not only the tool-use but also the end-state of the action sequence should be observable. The imitator may then acquire a meaning of the observed hand-tool motion in

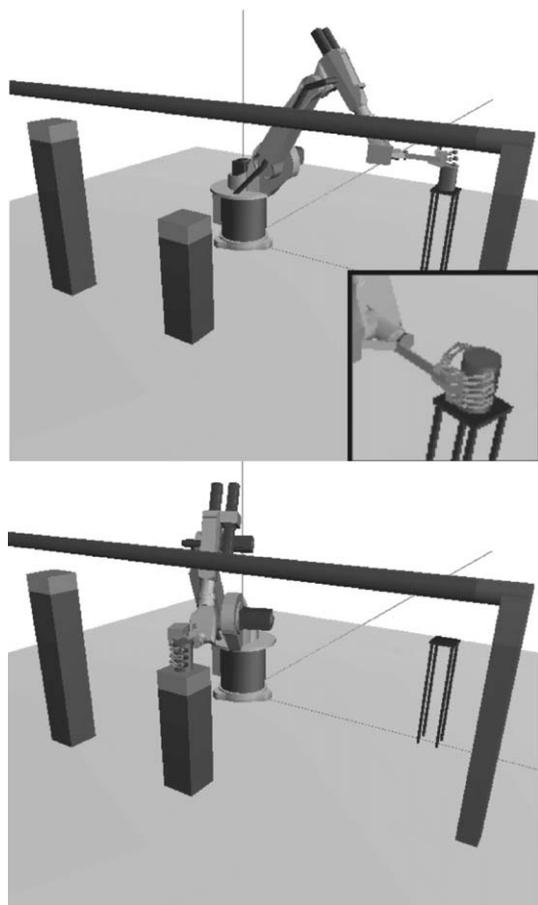


Fig. 7 – To illustrate the overt behavior in the inference task of Fig. 10, two snapshots of the robot simulator are shown.

the sense of a goal-directed action by covertly using his/her own motor representations for achieving the observed end-state. In the model, the activation peak in PFC representing the goal triggers the associated representation of means in PF. Subsequently, synaptic links are established with the tool-use representation in STS through the correlation based learning rule (see Appendix A.2). To guarantee that the resulting matching between action observation and action execution is indeed goal-directed, the learning epochs are defined by an internally generated reinforcement signal representing the successful planning of a posture sequence toward the desired goal posture (see Montague and Sejnowski, 1994 for a discussion of physiological mechanisms underlying such a permissive gating).

In Fig. 8, the result of the learning is shown in a simulation of an inference task in which only the grasping with the tool is directly observable. Through the reinforced STS-PF connections, the visual description of the hand-tool motion can be understood as functionally congruent to the AG-grip normally used by the observer to place the object at the higher target.

The conditions under which learning in the model takes place may also explain that in previous monkey studies tool-use mirror neurons have not been described (Rizzolatti et al., 1996; but see Arbib and Rizzolatti, 1999). The experiments may have simply lacked the multiplicity of similar observations

necessary to represent the new motor act in area STS. In addition and very important for our goal-directed theory of imitation, the observed end-state of the tool-use most likely had no specific meaning for the monkey and could thus not be associated with any behavior in the motor repertoire. Consistent with this view, Fogassi and colleagues (Ferrari et al., 2005) reported that during the new experiments the tool was also used to give food to the monkey.

Of course, this form of learning does not imply that the observer is also able to reproduce the tool-use. Our basic assumption that the agents do not necessarily share the same morphology explicitly excludes the possibility for a matching on the movement level which is the basis of many approaches for motor learning through imitation (Schaal et al., 2003). However, it has been suggested that more abstract knowledge may be acquired through observation by copying not the surface behavior but the organizational structure of the witnessed action (Byrne and Russon, 1998). Imagine, for instance, that the height of the bridge or the height of one of the goals is changed. The observer still can identify the goal but does not know what combination of means can be chosen to reproduce it. One possible strategy could be trying to copy the sequence of means used by the demonstrator. This can be achieved through a direct matching with congruent movement primitives in PF and F5 which in turn will bias the trajectory planning toward the desired goal postures. If the planning turns out to be successful, the observed response strategy can be associated with the goal by the learning procedure described above. If not, the trajectory planning has to be repeated in a much larger state-action space (see Supplementary Fig. 1 online for a model simulation).

It is important to note that this kind of learning through observation on the level of primitives is not restricted to the simplified case with only two categorical choices for grip and trajectory. Other grasping behaviors (e.g., a precision grip) and hand trajectories (e.g., a trajectory circumventing the obstacle at one side) not used before in the bridge paradigm could be copied as well whenever the respective movement primitives are already in the motor repertoire of the observer.

3. Discussion

When observing others in action with the intention to imitate the actions, we most likely do not encode the full detail of their motions but our interpretation of those motions in terms of the demonstrators' goal. The experimental literature reviewed in this article suggests the existence of a distributed representational system which allows one to “construct” the meaning of actions combining sensory evidence about environmental changes, situational context, prior task knowledge, and a matching between the observation and execution of action. The main objective of the present study was to formalize a dynamic model of this distributed representational system and to test it in several variations of a basic grasping-placing task.

3.1. Goal-directed imitation

In the goal-directed theory of imitation proposed by Bekkering and colleagues, imitative behavior can be considered

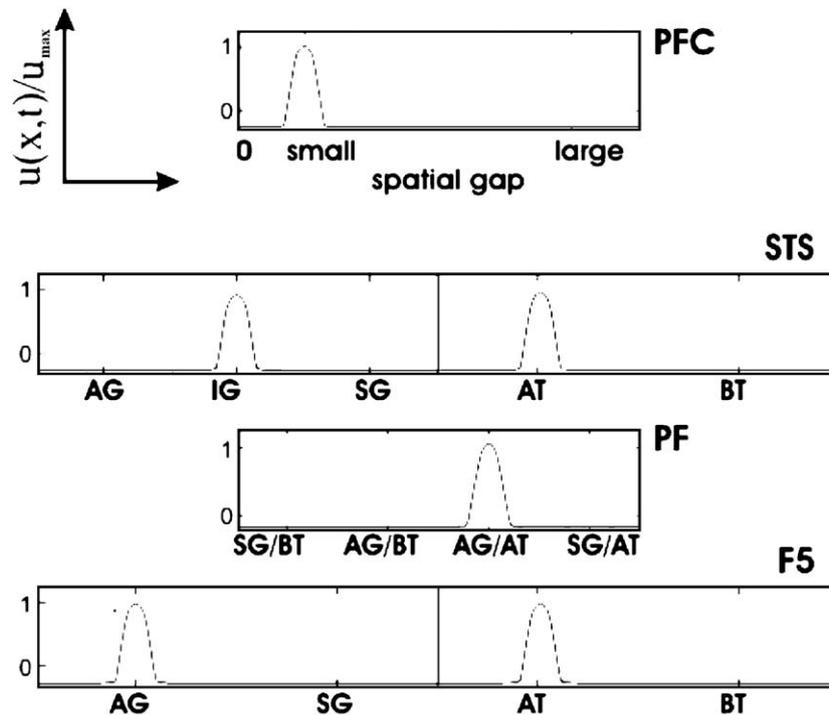


Fig. 8 – Learning to understand an action sequence with a tool grip which is not in the motor repertoire of the observer. In each layer, the dynamics has relaxed to a stable activation pattern. The tool grip displayed by the demonstrator is assumed to be visually classified and represented as a new grip type IG in area STS. An association is then learned between this new category and the action sequence AG/AT usually used by the demonstrator to reproduce the action effect. As a result of the learning, the IG-representation may directly drive neurons encoding the goal-directed sequence of primitives.

successful whenever the end-state of the observed action is reproduced. The means, on the other hand, may or not coincide with the observed ones. There is a need for some cognitive control whenever an automatic imitation of the means would lead, for instance, to a collision with an obstacle. But also in the case that a direct, congruent matching would be in principle possible, the imitator should not automatically adapt a response strategy which has been successfully associated with the goal in previous trials. In the proposed dynamic model, the primacy of the goals over the means is implemented by assuming that the goal representations in PFC evolve faster compared to the representations in the observation layer STS (Fig. 2). As a consequence, the selection of means in the areas PF of the inferior parietal lobule is biased by the goal representations. However, this temporal advantage manifests only if the observer is familiar with the task and thus has prior expectations about how the goals and their associated means could look like. Experimental paradigms which directly manipulate the prior task information are therefore expected to reveal further insights about the relative timing of processing in STS, PF and PFC. To explain reaction time data in pointing tasks, we have recently used a conceptually related model in which the preshaping of target representations varied dynamically in accordance with the probability of target occurrence (Erlhagen and Schöner, 2002). For a more complex grasping-placing task, the dynamic model for goal-directed imitation predicts that for rare goals the imitator will copy a change in the observed means (e.g., the demonstrator adapts the grasping behavior from one trial to

another) with higher probability compared to more frequently experienced goals.

In dynamic and cluttered environments, very often, sensory information about the crucial final part of an action sequence displayed by another agent may not be available. As the model simulations of the bridge paradigm show, a goal-directed organization of action means in IPL together with the integration of prior task knowledge may allow inferring the demonstrator's action goal when only the grasping part of the action is directly observable. The only crucial assumption is that the observed grasping triggers the same sequence of primitives which is also activated during the execution of the complete goal-directed action. The recent discovery of mirror neurons for grasping in area PF/PFG (Fogassi et al., 2005), which discharge according to the final goal of the action, strongly supports the biological plausibility of the model architecture.

The functional role of the action organization in IPL may be phrased within the framework of internal forward models for predicting the sensory consequences of a motor act. Wolpert et al. (2003) have recently suggested to extend the concept of internal models to a more abstract level somewhat independent of specific movement trajectories. The key idea behind the proposed computational scheme (HMOSAIC model) is to include hierarchically higher levels of motor control in the simulation loop for action understanding. On this view, the goal-directed mirror neurons in IPL may be seen as being part of an abstract forward model for interpreting an ongoing action.

Since the pathway for inference involves the additional mappings from STS to PF and subsequently to the goal representations in PFC, the model predicts a delayed path planning compared to the case when the goal representation is directly triggered by visual input. This prediction could be tested in reaction time studies of an imitation task in which either the action goal (e.g., a hand moving away from a placed object) or action means (e.g., the grasping of the object with a specific grip) are given as a cue.

In the model, the goal-directed selection of means in areas PF is translated via congruent mappings to the premotor area F5. There, the representations of the motor primitives serve to constrain the motor planning toward the goal postures by selecting areas in posture space compatible with these primitives. In visually guided grasping of objects, other pathways not included in the present model may provide area F5 with more detailed information to further constrain the planning. In particular, the projections from area AIP in parietal cortex are believed to transmit information about object shape and size needed for hand shaping (for review, see [Rizzolatti and Luppino, 2001](#); for a neurocomputational approach, see the FARS model [Fagg and Arbib, 1998](#)).

3.2. Neuronal population representations

In each model layer, instances of a particular category are represented by localized activation patterns. This is consistent with the idea of population coding. Individual neurons of a certain subpopulation represent task-specific information to a greater or lesser degree depending on the functional distance to the instance coded by them. The notion of similarity implicitly assumes that the internal representation space is endowed with metric structure. For high-dimensional, abstract spaces defining categories like for instance grip type or trajectory type, the metric distance between any two instances is not directly observable ([Edelman and Duvdevani-Bar, 1997](#)). However, it may still be defined operationally by the degree of overlap of their neuronal representations. The bridge paradigm with its need to choose specific grasping and transporting behaviors to achieve a certain goal suggests disjoint representations of the means in each layer of the mirror circuit. For a more general paradigm, it would be interesting to directly test on the neuronal level of the metric structure of the motor vocabulary.

Interestingly, [Ferrari et al. \(2005\)](#) described in their recent tool-use study, firing patterns of mirror neurons in F5 consistent with the competition process implemented in the model. Tool-responding mirror neurons appeared to be inhibited when the monkey observed the experimenter grasping with the hand. This response pattern may be explained by assuming inhibitory interactions with a subpopulation of classical hand-responding mirror neurons.

In line with the notion of preshaping of neuronal representations, recent neurophysiological findings reveal that neurons involved in the planning of goal-directed hand or eye movements may selectively change their activity in relation to prior task information (e.g., [Bastian et al., 2003](#); [Erlhagen et al., 1999](#); [Doris and Munoz, 1998](#); for an overview, see [Gold and Shadlen, 2002](#)). Moreover, [Asaad et al. \(2000\)](#) described cell populations in PFC which showed modulations

in the baseline firing rates in dependence of which task had to be performed. The authors speculate that this modulation may provide the means to bias decision processes in other brain areas. In line with this hypothesis, our modeling results suggest that the preshaping of populations in PFC may implement a simple temporal mechanism for an intentional control of the direct matching pathway.

3.3. Learning the goal-directed matching

[Oztop and Arbib \(2002\)](#) have recently extended the FARS model ([Fagg and Arbib, 1998](#)) representing circuitry for a visually guided grasping of objects to include also pathways for action recognition. The authors hypothesize that the basic functionality of the F5 mirror system is to provide the appropriate feedback for the grasping. In their model, a neural network was trained to map the “hand state” representing hand configuration parameters and parameters relating hand and object onto motor neurons coding for the respective grip type. Since the hand-state input may be generalized from one’s own hand to the hand of others, this learned mirror pathway may be used to recognize grasping acts performed by a demonstrator. Also in our model, we assume that first a congruent mapping between the visual and the motor description of a particular action is learned during self-observation. This congruent mapping is then generalized to the movements of others. The proposed model thus covers more common action observation/execution paradigms in which a direct matching between congruent motor primitives is possible (e.g., a grasping–placing sequence without obstacle). However, in contrast to the model of [Oztop and Arbib](#), the learning signal is not the motor program associated with a particular primitive but a motor planning signal representing whether or not selected primitives can be used to achieve the desired goal. The feedback from this “simulation stage” gates the correlation-based learning of synaptic links. The resulting goal-directed matching in the mirror circuit allows developing an understanding of an action also in cases where a congruent mapping is not possible due to differences in embodiment, in task constraints or in motor skills. There is no doubt that for humans incongruence in movement and effector does not impair the capacity of inferring goals. The discovery of the tool-use mirror neurons strongly suggests that under appropriate experimental conditions also monkeys may develop the abstract motor representations necessary for this capacity.

The emphasis on goal-directed matching does of course not exclude that, for other purposes (e.g., motor learning), a matching on the level of kinematics may be crucial. In the context of robotics research, [Dautenhahn and colleagues \(Alissandrakis et al., 2002\)](#) proposed a theoretical framework for solving the “correspondence problem” between model and imitator. In their application, the authors used different metrics to measure successful imitation with different granularity ranging from the movement level to the goal level.

In a shared common context, an imitator may benefit from an experienced model by copying the observed sequence of means which, however, has to be “confirmed” using the proper planning in posture space. If successful, the specific action means are linked via Hebbian learning to the

goal representation in the prefrontal cortex. Since the planning requires an anticipated goal posture, this form of learning by imitation explicitly requires an interpretation of the observed motor pattern as a goal-directed behavior. Consistent with this model prediction, an interaction between the mirror circuit and area 46 of PFC has been described in a recent fMRI study of imitation learning (Buccino et al., 2004).

The following experimental test could nicely illustrate that the learned link to the goal is crucial. Assume that the bridge obstacle is removed for the model but not for the imitator. Now the demonstrator may grasp the object from the side. For the imitator, an automatic copy of the SG-grip would result in a collision with the bridge (Erlhagen et al., *in press*).

Findings in a recent monkey study have been interpreted as evidence for a purely perceptual basis of action understanding. Perrett and colleagues (Jellema et al., 2000) described cell populations in STS which seem to encode not only the action per se but also the intentionality of that action (e.g., grasping the object on the right and not the object on the left). The firing patterns are consistent with the notion that in a known task setting pure visual cues like for instance the direction of hand movement may be sufficient to predict the consequence of an ongoing action. However, we argue here that an observer may develop such high-level visual representations only after the action is understood, that is, the relation between goal and means has been established using the own motor repertoire. Subsequently, direct links between the high-level visual representations in STS and the goal representations in PFC may be learned to allow for anticipating the action consequences before the action is completed. This prediction is in line with experimental findings showing that certain cell populations in PFC, which first are triggered by a goal (reward), tend to become activated with experience by cues that predict that goal (Miller, 2000).

3.4. Outlook

For the present modeling study, we have chosen a paradigm in which the action goal is a simple physical end-state. However, the model architecture may be extended to include also the activation of higher intentional goals by observed gestures. For instance, when you observe someone grasping a glass of water you may use your own behavioral repertoire to infer not only the mouth as the physical end-state of the action but also that the person is thirsty. Indeed, it has been suggested that the basic processing principles implemented in our dynamic model represent a precursor for a more general social-understanding ability (Gallese and Goldman, 1998).

4. Experimental procedures

4.1. Experimental paradigm

For our modeling study, we adopt a paradigm, which has been developed to further investigate in experiments with humans the idea that actions are organized in a goal-directed manner (van Schie and Bekkering, *in preparation*). The paradigm contains an object that must be grasped and then

placed at one of two laterally presented targets that differ in height. The possible hand trajectories are constrained by the fact that an obstacle in the form of a bridge has to be avoided (Fig. 9). The task differs in two important aspects from typical paradigms, which have been used in the past to investigate the impact of action observation on action execution. In studies leading to the discovery of the mirror system in non-human primates, the action goal was defined as a simple hand-object interaction whereas in the present task the goal is defined as the end-state of the action sequence, that is, the placing of an object at a particular position. The bridge paradigm differs also from recently used grasping-placing tasks with human subjects (Chaminade et al., 2002; Wohlschäger et al., 2003) in that the ultimate goal imposes strong restrictions on how to grasp and transport the object. Depending on the height of the bridge, the lower target may only be reached by grasping the object from the side and transporting it below the bridge. Placing the object at the higher target, on the other hand, may require combining a grasping from above and a hand trajectory above the bridge.

We use this experimental design for imitation tasks in which the observer (e.g., a robot) has to reproduce the visually perceived or inferred effect of an action sequence displayed by a model with different embodiment (e.g., a human). A detailed modeling of the visual pathway goes beyond the scope of this article. We therefore assume that an appropriate input triggers the neuronal populations in model layers representing the grip type and the goal (but see Erlhagen et al., *in press* for a model application in a real robot-human task).

4.2. Model architecture

In the following, we summarize experimental findings, which constrain the choice of the model architecture and the nature

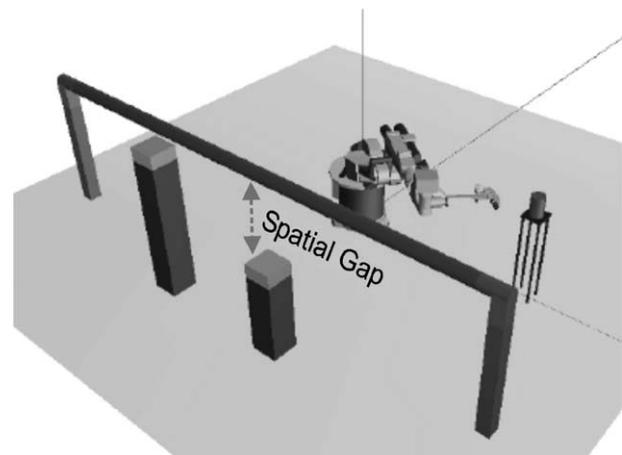


Fig. 9 – Sketch of the experimental paradigm with a cylindrical object to be grasped, the obstacle in form of a bridge and the two possible placing targets of different height. The artificial arm/hand system has to imitate the action effect of a grasping-placing sequence demonstrated by a model with different embodiment (e.g., a human). The grasping and transporting behavior is constraint by the magnitude of the spatial gap between placing target and bridge.

of the internal representations used to model imitative, goal-directed behavior.

An important characteristic of mirror neurons is that they code for hand-object interactions irrespective of the precise physical aspects of the movement. Some mirror neurons generalize even across the end-effector used (Rizzolatti et al., 1996). This coded level of abstraction has been conceptualized by introducing the notion of a vocabulary of motor primitives (Rizzolatti and Gentilucci, 1988) or motor schema (Arbib, 1981). Subpopulations of neurons in the premotor area F5 are thought to represent distinct goal-directed motor acts such as for instance grasping, holding or placing an object. Perrett and colleagues described neurons with strikingly similar firing characteristics with respect to hand-object interactions in the superior temporal sulcus (STS) of macaque (for a review, see Carey et al., 1997). The major difference to the mirror neurons in F5 is that the goal-related neurons in STS do not discharge during active movements. With respect to the direct matching hypothesis, this suggests that neuronal populations in STS may provide a visual description of a goal-directed action, which is then mapped onto a similar motor representation in F5. For the modeling, we adopt the idea of separate action observation and action execution layers in which neuronal populations encode abstract motor primitives. Concretely for our bridge paradigm, we distinguish for each of the two parts of the action sequence two possible response alternatives. The direct hand-object interaction may be accomplished by grasping the object from above or from the side (in the following referred to as AG-grip or SG-grip, respectively). The transporting-placing phase of the sequence is characterized by the strategy how the obstacle is avoided. We assume that distinct subpopulations of neurons encode either the trajectory above or the trajectory below the bridge (in the following termed AT-trajectory and BT-trajectory, respectively). Areas F5 and STS are only indirectly connected through anatomical projections to areas PF/PFG (termed PF hereafter) in the inferior parietal lobule (IPL). Area PF also contains mirror neurons (Rizzolatti et al., 2001) and may thus be seen as an intermediate stage of the observation/execution matching circuit. The STS-PF and the PF-F5 connections are reciprocal allowing for a flow of information from action observation to action execution and vice versa. Fig. 10 gives a schematic view of the model architecture with the mirror circuit as one part.

Important for the emphasized goal-directedness of imitation is the fact that IPL has strong anatomical connections with the prefrontal cortex (for review, see Rizzolatti and Luppino, 2001) which is believed to subserve the organization of means for goal-directed behavior in other brain areas (Pochon et al., 2001; Quintana and Fuster, 1999; Miller, 2000). This planning function suggests that a goal representation in PFC may bias the processing in area PF toward the selection of a sequence of motor primitives appropriate for the achievement of that intentional goal. Direct evidence for a goal-directed organization of actions in area PF has been gained in a recent monkey study. Using a grasping-placing paradigm, Fogassi et al. (2005) described a population of grasping neurons in PF which showed a selective response in dependence of the final goal of the action (eating vs. placing). Adapted to the bridge paradigm, this finding suggests that neuronal representations of the action goals should be directly connected with subpopula-

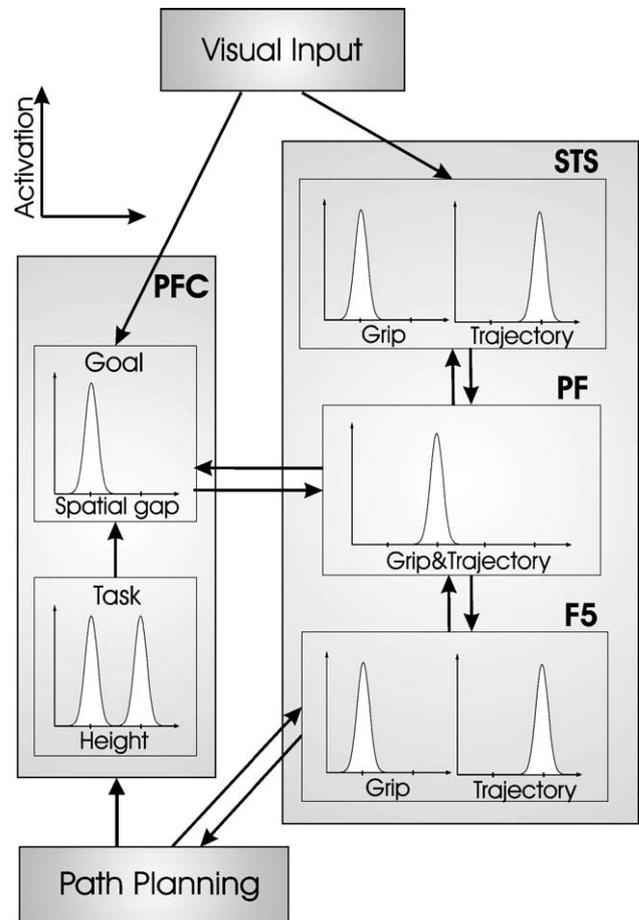


Fig. 10 – Schematic view of the model architecture. The core part consists of the STS-PF-F5 circuit for a matching of action observation and action execution which is reciprocally connected with a layer in prefrontal cortex. This “goal layer” encodes the intentional action goal parameterized by its spatial gap relative to the bridge. The demonstrated means, the selected goal and the selected grip and trajectory type are represented within the network by self-stabilized activity patterns of local pools of neurons. The bimodal activity distribution in the “task layer” of PFC reflects the memorized information about the two (equally likely) placing targets characterized by their height. Layer F5 is directly connected with the planning system which provides the goal-directed posture sequence for the arm/hand system. The path planning also provides an internal feedback signal for the learning of the goal-directed associations in the mirror system (see the learning section below).

tions in layer PF encoding specific combinations of movement primitives (i.e., AG/AT, AG/BT, SG/AT or SG/BT).

Beside its role in the organization of forthcoming actions, it is commonly believed that PFC plays a crucial role in the integration of goal-relevant information. There is striking evidence from neurophysiological studies that associative relationships between anatomically segregated neuronal populations in PFC allow to integrate prior task knowledge, knowledge about environmental constraints and sensory cues (for review, see Miller, 2000). In the model architecture,

we represent this integrative role of PFC by assuming (1) that the visual cue (e.g., a hand moving away from the placed object) processed in connected association areas of the visual pathway triggers the representation of the desired goal, and (2) that in a second layer, prior task knowledge (i.e., the identity of all possible targets in terms of their height) is stored (Fig. 10). The functional role of this task layer is to provide a constant input to the system resulting in a “priming” of all possible goals and their associated means. This reflects the fact that in a known task setting the imitator can engage in partial (motor) preparation even before the observation of the model.

It is important to stress that the assumed mapping from cue to goal mirrors the task contingencies of an imitation paradigm. The target chosen by the demonstrator defines the desired end-state. A different task, which might emphasize, for instance, the importance of a complementary behavior, would require a mapping to the target not chosen by the model.

The existence of the bridge as an environmental constraint does not directly affect the action goal but strongly the means that can be chosen. This impact of the environmental constraint is reflected in the model by how the goals are parameterized. We assume subpopulations that encode the height of the placing targets relative to the height of the bridge. Depending on the spatial gap between bridge and target, particular means may be excluded from use (e.g., a trajectory below the bridge in case of very similar heights) and consequently no associations to their representations in area PF are learned.

When attempting to reproduce the observed action effect, the abstract motor representations in F5 have to be translated in lower motor structures into a movement plan generating the right kinematics. As discussed in detail below (see the learning section), this planning stage is also assumed to provide a feedback signal for establishing the goal-directed organization of synaptic links in the network.

In line with findings of recent behavioral and neurophysiological studies (Rosenbaum et al., 2001; Graziano et al., 2002), we assume that planning takes place in posture space. A collision-free path for the robot arm is generated from the initial posture to the postures representing the grasping and subsequently the placing of the object. Importantly, the abstract representations in the mirror system are directly linked to the planning stage since the movement primitives in F5 serve to preselect relevant parts of the posture space. This makes a real-time planning in the high-dimensional space feasible. The selection of goal postures prior to the movement requires that during development and practice associations have been formed between the visual image of the arm in a large number of configurations and the corresponding joint angles. It has been suggested that the spontaneous arm-waving and simultaneous watching of newborn babies may be essentially a mechanism for learning these associations (van der Meer et al., 1995).

Ideas from the field of dynamic programming have inspired the concrete path-planning algorithm including the obstacle avoidance. The details are mainly determined by the need to allow for the control of a robot arm in real time (compare Erlhagen et al., in press and Supplementary note online for further details).

4.3. Model details

Our modeling approach is constrained by two basic hypotheses. First, it is assumed that the task relevant information in each model layer of the distributed network is encoded by means of sustained activity in local pools of neurons. Stabilizing and maintaining goal-related information are essential capacity whenever the persistence toward a goal in noisy environments with distracting events is required. Such actively maintained representations are also thought to underlie the formation of associations between events that are separated in time (Hebb, 1949; for review, see Bi and Poo, 2001).

Neuronal activity, which persists after cessation of an inducing event, is observed in many brain areas including parietal cortex, prefrontal cortex, premotor and motor cortex (for an overview, see Durstewitz et al., 2000). Types of neurons involve “memory cells” for sensory cues or abstract rules in PFC (Miller, 2000) but also mirror neurons in areas PF and F5. Typically, grasping or placing neurons continue firing at an elevated rate for an extended period subsequent to the defining event (Rizzolatti et al., 2001).

In many network models, persistent activity arises from reverberatory excitation within local populations of neurons, which is effectively counterbalanced by inhibitory feedback loops (for reviews, see Wang, 2001; Durstewitz et al., 2000). In addition, it is frequently assumed that the interactions are spatially structured with excitation dominating at small distances and inhibition in the surround. Such a spatially organized interaction scheme has been originally proposed to explain localized activation patterns in small pieces of neuronal tissue (Wilson and Cowan, 1973; Amari, 1977). It has later been applied to model various functionalities in the perceptual and the motor domain (e.g., Kopecz and Schöner, 1995; Ben-Yishai et al., 1995; Zhang, 1996; Jancke et al., 1999;

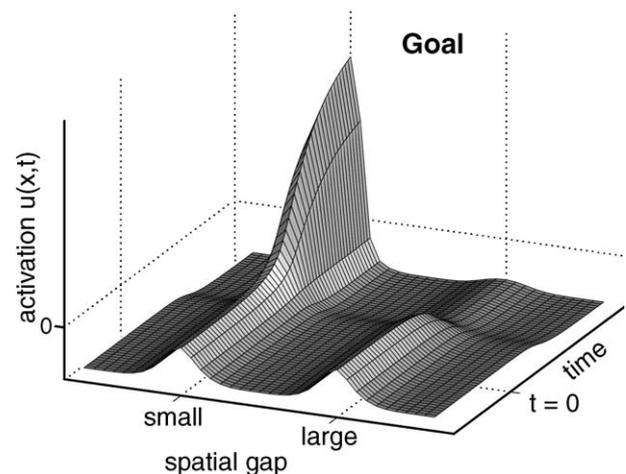


Fig. 11 – The evolution of a self-stabilized activation pattern in the goal layer of PFC is shown. The pattern represents the selection of the higher target (i.e., small gap) as the action goal. Time $t = 0$ defines the onset of the visual input. Note that at that time the system appears to be already preshaped by the constant input from the task layer. The zero activation level defines the threshold for the ignition of the self-stabilized population response.

Kang et al., 2003). For the present modeling work, we adopt for each network layer a center-surround organization of recurrent interactions as a well studied mechanism underlying persistent activity patterns. In addition, subpopulations coding for different categorical choices (e.g., AG-grip and SG-grip) are assumed to interact purely inhibitory with each other leading to a competition between response alternatives.

As a second hypothesis constraining the modeling work, we assume that the specification of goals and means is a continuous process that is sensitive to a host of behaviorally relevant factors such as sensory evidence, general task information and prior probabilities. The accumulation of information is thought to take place over a limited time period after which a decision for one of the possible alternatives is made (Gold and Shadlen, 2002; Erlhagen et al., 1999). To model this process, we assume that the various local networks are bi-stable. In this dynamic regime, a stable state in which all neurons fire at a rate close to resting level coexists with the state of a self-sustained activity pattern (Amari, 1977; Erlhagen et al., 1999; Buccino et al., 2004; Compte et al., 2000). Functionally, this allows preactivating local populations close to the threshold for the ignition of an active response by means of weak external inputs. Despite the relatively small change in activation, this “preshaping” mechanism may have a drastic effect on the time course of the specification process in a local network (Erlhagen, 2003; Erlhagen and Schöner, 2002). This in turn may affect the decision processes in connected layers of the distributed network (compare Section 3).

In Fig. 11, we exemplify the integration-decision process by showing the evolution of a self-stabilized activation peak in the goal layer representing the selection of the higher target parameterized by the smaller spatial gap (Fig. 9). Note that the constant task input has already preshaped the representation at the time $t = 0$ of the onset of the specifying visual input. The network dynamics in each layer is governed by a “standard” firing rate model representing the average level of activity in a population of excitatory and inhibitory neurons (Dayan and Abbott, 2001, see Appendix A.1 for details).

The learning of synaptic connections between neuronal populations in any two layers of the model network is based on Hebbian learning (for review, see Bi and Poo, 2001; for discussion of theoretical aspects, see Dayan and Abbott, 2001). Recently, Keyzers and Perrett (2004) have suggested that a correlation-based learning rule within the STS-PF-F5 circuit may explain how mirror properties may evolve. In addition, we propose that also the synaptic links of area PF to the goal representations in PFC may develop using such biologically plausible rules.

A basic assumption is that the time scale of the synaptic modification is small compared to the time scale of the neuronal dynamics. The synaptic efficiency can thus be treated as constant on the fast time scale of the pattern formation. When the network has relaxed to a stable state, a Hebb rule is applied during a developmental period defined by an internal reinforcement signal (for details see Appendix A.2). Note that the transient phase of the dynamics could have been included in the learning process as well without qualitatively changing the results presented here. Fig. 12 sketches the connections $a(x,y)$ between neurons in two distinct network layers which are modified during practice. The synaptic connections $w(x,x')$

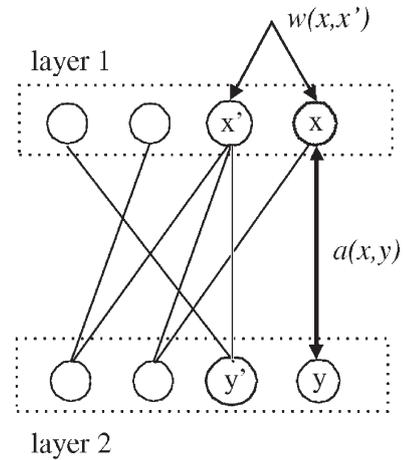


Fig. 12 – Sketch of the connectivity within layers, $w(x,x')$, and between layers, $a(x,y)$, of the model network.

between any two neurons within the same layer remain fixed and are chosen to guarantee the bi-stable behavior of the layer dynamics.

Acknowledgments

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Appendix A

A.1. Mathematical details of the firing rate model

In each network layer, the activity $u(x, t)$ of a neuron x at time t is described by the following equation:

$$\tau \frac{\delta}{\delta t} u(x, t) = -u(x, t) + g(u(x, t)) \left[\int w(x - x') f(u(x', t)) dx' - w_{\text{inhib}} \int f(u(x', t)) dx' \right] + h + \sum_i S_i(x, t)$$

where the constants $\tau > 0$ and $h < 0$ define the time scale and the resting level of the dynamics, respectively. The firing rate $f(u)$ is taken as a non-linear function of sigmoid shape

$$f(u) = \frac{1}{1 + \exp(-\beta(u - u_f))}$$

with threshold u_f and slope parameter β . The excitatory connections, $w(x, x') = w(x - x')$, between nearby neurons are modeled as a Gaussian profile with standard deviation σ and amplitude A

$$w(x, x') = A \exp\left(-\frac{(x - x')^2}{2\sigma^2}\right).$$

The feedback inhibition depends on the overall activity level in the network and is controlled by the constant w_{inhib} .

The gating signal $g(u)$ is modeled by a sigmoidal function with threshold $u_g > u_f$ (Jancke et al., 1999). This choice ensures that the recurrent interactions dominate the processing only if the connected neurons are sufficiently activated above resting level by external inputs. The values of the diverse model parameters are chosen to ensure the bi-stability of the dynamics (Amari, 1977). For simplicity, the identical set is used for all layers of the network.

Finally, the term $\sum_i S_i(x,t)$ describes the summed input from other model layers and sources external to the network. Since an explicit modeling of the visual pathway goes beyond the scope of the present study, Gaussian functions of appropriate strength are used for simplicity as visual inputs triggering the population representations in the goal layer and in layer STS. These Gaussian inputs are kept fixed for all model simulations shown in this paper.

A.2. Synaptic modification rule

The equation for the correlation-based synaptic modification between neuron x in layer 1 and neuron y in layer 2 is given by (compare Fig. 12):

$$\tau_s \frac{\delta}{\delta t} a(x,y,t) = -a(x,y,t) + \eta f(\bar{u}_1(x))f(\bar{u}_2(y)) \quad (1)$$

where \bar{u}_1 and \bar{u}_2 denote the equilibrium solutions of the relaxation phase in layer 1 and layer 2, respectively, η defines a scaling parameter, $\tau_s \gg \tau$ the time scale and f is the sigmoidal threshold function. Note that the activity patterns coding for the distinct, categorical choices in each network layer are assumed to be non-overlapping such that the strength $a(x,y,t)$ is not affected by the representation of alternative means or goals. The time window for the learning is defined by an internally generated reinforcement signal representing a successful path planning. Technically, we implement the monitoring process by multiplying the right hand side of Eq. (1) with a function that takes on for simplicity the value 1 during the learning period and the value 0 otherwise. At the end of the learning process, the synaptic strength $a(x,y,t)$ becomes the time-independent $A(x,y)$:

$$A(x,y) = \eta f(\bar{u}_1(x))f(\bar{u}_2(y)). \quad (2)$$

Since the self-stabilized activity patterns \bar{u}_1 and \bar{u}_2 are symmetric and bell-shaped, also the evolving connection profile is symmetric with maximum connection strength to the maximum excited neuron in the other layer. The equilibrium solution in layer 1 (equivalently for layer 2) is then given by:

$$\bar{u}_1(x) = \int w(x-x')f(\bar{u}_1(x'))dx' + h + S_2(x) \quad (3)$$

with the input from layer 2

$$S_2(x) = \int A(x,y')f(\bar{u}_2(y'))dy'.$$

For the model simulations, the strength of the learned synaptic connections between layers is adjusted using the parameter η . Depending on whether or not an existing activation pattern should drive the evolution of suprathreshold activity in a subsequent layer or should only preshape

neuronal representations, its effective input strength is chosen above or slightly below the threshold A_{TH} for the ignition of an active response (Erlhagen and Schöner, 2002).

Appendix B. Supplementary data

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.brainres.2006.01.114.

REFERENCES

- Alissandrakis, A., Nehaniv, C.L., Dautenhahn, K., 2002. Imitation with ALICE: learning to imitate corresponding actions across dissimilar embodiments. *IEEE Trans. Syst. Man Cybern., Part A, Syst. Humans* 32, 482–496.
- Amari, S., 1977. Dynamics of pattern formation in lateral-inhibitory type neural fields. *Biol. Cybern.* 27, 77–87.
- Amit, D.J., Brunel, N., 1997. Model of global spontaneous activity and local structured activity during delay periods in the cerebral cortex. *Cereb. Cortex* 7, 237–252.
- Arbib, M.A., 1981. Perceptual structures and distributed motor control. In: Brook, V.B. (Ed.), *Handbook of Physiology—The Nervous System*. American Physiological Society, pp. 1449–1480.
- Arbib, M.A., Rizzolatti, G., 1999. Neural expectations. A possible evolutionary path from manual skills to language. In: Van Loocke, P. (Ed.), *The Nature of Concepts. Evolution, Structure and Representation*. Routledge, New York, pp. 128–154.
- Assad, J.A., Maunsell, J.H.R., 1995. Neuronal correlates of inferred motion in primate posterior parietal cortex. *Nature* 373, 518–521.
- Asaad, W.F., Rainer, G., Miller, E.K., 2000. Task-specific neural activity in the primate prefrontal cortex. *J. Neurophysiol.* 84 (1), 451–459.
- Bastian, A., Schöner, G., Riehle, A., 2003. Preshaping and continuous evolution of motor cortical representations during movement preparation. *Eur. J. Neurosci.* 18, 2047–2058.
- Bekkering, H., Wohlschläger, A., Gattis, M., 2000. Imitation of gestures in children is goal-directed. *Q. J. Exp. Psychol.* 53A, 153–164.
- Ben-Yishai, R., Bar-Or, R.L., Sompolinsky, H., 1995. Theory of orientation tuning in visual cortex. *Proc. Natl. Acad. Sci. U. S. A.* 92, 3844–3848.
- Bi, G., Poo, M., 2001. Synaptic modification by correlated activity: Hebb's postulate revisited. *Annu. Rev. Neurosci.* 24, 139–166.
- Buccino, G., Vogt, S., Ritzl, A., Fink, G.R., Zilles, K., Freund, H.-J., Rizzolatti, G., 2004. Neural circuits underlying imitation learning of hand actions: an event-related fMRI study. *Neuron* 42, 1–20.
- Byrne, R.W., Russon, A.E., 1998. Learning by imitation: a hierarchical approach. *Behav. Brain Sci.* 21 (5), 667–684.
- Carey, D.P., Perrett, D.I., Oram, M.W., 1997. Recognizing, understanding and reproducing action. In: Jeannerod, J., Grafman, J. (Eds.), *Handb. Neuropsychol.*, vol. 11. Elsevier Science, Amsterdam, pp. 111–130.
- Chaminade, T., Meltzoff, A.N., Decety, J., 2002. Does the end justify the means? A PET exploration of the mechanisms involved in human imitation. *NeuroImage* 15, 318–328.
- Compte, A., Brunel, N., Goldman-Rakic, P.S., Wang, X.J., 2000. Synaptic mechanisms and network dynamics underlying spatial working memory in a cortical network model. *Cereb. Cortex* 10, 910–923.
- Dautenhahn, K., Nehaniv, C.L., 2002. The target-based

- perspective on imitation. In: Dautenhahn, K., Nehaniv, C.L. (Eds.), *Imitation in Animals and Artifacts*. MIT Press, Cambridge, MA, pp. 1–40.
- Dayan, P., Abbott, L.F., 2001. *Theoretical Neuroscience*. The Press MIT.
- di Pellegrino, G., Fadiga, L., Fogassi, L., Gallese, V., Rizzolatti, G., 1992. Understanding motor events: a neurophysiological study. *Exp. Brain Res.* 91, 176–180.
- Doris, M.C., Munoz, D.P., 1998. Saccadic probability influences motor preparation signals and time to saccadic onset. *J. Neurosci.* 18, 7015–7026.
- Durstewitz, D., Seamans, J.K., Sejnowski, T.J., 2000. Neurocomputational models of working memory. *Nat. Neurosci.* 3, 1184–1191.
- Edelman, S., Duvdevani-Bar, S., 1997. Similarity, connectionism, and the problem of representation in vision. *Neural Comput.* 9, 701–721.
- Erlhagen, W., 2003. Internal models for visual perception. *Biol. Cybern.* 88, 409–417.
- Erlhagen, W., Schöner, G., 2002. Dynamic field theory of movement preparation. *Psychol. Rev.* 109, 545–572.
- Erlhagen, W., Bastian, A., Jancke, D., Riehle, A., Schöner, G., 1999. The distribution of neuronal population activation as a tool to study interaction and integration in cortical representations. *J. Neurosci. Methods* 94, 53–66.
- Erlhagen, W., Mukovskiy, A., Bicho, E., Panin, G., Kiss, C., Knoll, A., H van Schie and Bekkering, H., in press. Goal-directed imitation for robots: a bio-inspired approach to action understanding and skill learning. *Robot. Auton. Syst.*
- Fagg, A.H., Arbib, M.A., 1998. Modeling parietal-premotor interactions in primate control of grasping. *Neural Netw.* 11, 1277–1303.
- Ferrari, P.F., Rozzi, S., Fogassi, L., 2005. Mirror neurons responding to observation of actions made with tools in monkey ventral premotor cortex. *J. Cogn. Neurosci.* 17, 1–15.
- Filion, C.M., Washburn, D.A., Gullledge, J.P., 1996. Can monkeys (*Macaca mulatta*) represent invisible displacement? *J. Comp. Psychol.* 110, 386–395.
- Fogassi, L., Ferrari, P.F., Gesierich, B., Rozzi, S., Chersi, F., Rizzolatti, G., 2005. Parietal lobe: from action organization to intention understanding. *Science* 308, 662–667.
- Gallese, V., Goldman, A., 1998. Mirror neurons and the simulation theory of mind-reading. *Trends Cogn. Sci.* 2, 493–501.
- Gold, J.I., Shadlen, M.N., 2002. Banburismus and the brain: decoding the relationship between sensory stimuli, decisions, and reward. *Neuron* 36, 299–308.
- Graziano, M., Taylor, S.A., Moore, S.R., Cooke, T., 2002. The cortical control of movement revisited. *Neuron* 36, 349–362.
- Hebb, D.O., 1949. *The Organization of Behavior: A Neurophysiological Theory*. Wiley, New York.
- Iacoboni, M., Woods, R.P., Brass, M., Bekkering, H., Mazziotta, J.C., Rizzolatti, G., 1999. Cortical mechanisms of human imitation. *Science* 286, 2526–2528.
- Iacoboni, M., Koski, L.M., Brass, M., Bekkering, H., Woods, R.P., Dubeau, M.C., Mazziotta, J.C., Rizzolatti, G., 2001. Reafferent copies of imitated actions in the right superior temporal cortex. *Proc. Natl. Acad. Sci. U. S. A.* 98 (24), 13995–13999.
- Jancke, D., Erlhagen, W., Dinse, H.R., Akhavan, A.C., Giese, M., Steinhage, A., Schöner, G., 1999. Parametric population representation of retinal location: neuronal interaction dynamics in cat primary visual cortex. *J. Neurosci.* 19, 9016–9028.
- Jellema, T., Baker, C.I., Wicker, B., Perrett, D.I., 2000. Neural representation for the perception of the intentionality of actions. *Brain Cogn.* 44, 280–302.
- Kang, K., Shelley, M., Sompolinsky, H., 2003. Mexican hats and pinwheels in visual cortex. *Proc. Natl. Acad. Sci. U. S. A.* 100, 2848–2853.
- Keysers, C., Perrett, D.I., 2004. Demystifying social cognition: a Hebbian perspective. *Trends Cogn. Sci.* 8, 501–507.
- Kopecz, K., Schöner, G., 1995. Saccadic motor planning by integrating visual information and pre-information on neural, dynamic fields. *Biol. Cybern.* 73, 49–60.
- Meltzoff, A.N., 1995. Understanding the intentions of others: re-enactment of intended acts by 18-months-old children. *Dev. Psychol.* 31, 838–850.
- Miller, E.K., 2000. The prefrontal cortex and cognitive control. *Nat. Rev.* 1, 59–65.
- Montague, P.R., Sejnowski, T.J., 1994. The predictive brain: temporal coincidence and temporal order in synaptic learning mechanisms. *Learn. Mem.* 1, 1–33.
- Oztop, E., Arbib, M.A., 2002. Schema design and implementation of the grasp-related mirror neuron system. *Biol. Cybern.* 87, 116–140.
- Pochon, J.B., Levy, R., Poline, J.B., Crozier, S., Lehericy, S., Pillon, B., Dewer, B., Le Bihan, D., Dubois, B., 2001. The role of dorsolateral cortex in the preparation of forthcoming actions: an fMRI study. *Cereb. Cortex* 11, 260–266.
- Quintana, J., Fuster, J.M., 1999. From perception to action: temporal integrative functions of prefrontal and parietal neurons. *Cereb. Cortex* 9, 213–221.
- Ritscher, J., Blake, A., Hoogs, A., Stein, G., 2003. Mathematical modeling of animate and intentional motion. *Philos. Trans. R. Soc. London, Ser. B* 358, 475–490.
- Rizzolatti, G., Gentilucci, M., 1988. Motor and visual-motor functions in premotor cortex. In: Rakic, P., Singer, W. (Eds.), *Neurobiology of the Neocortex*. Wiley, Chichester, pp. 269–284.
- Rizzolatti, G., Luppino, G., 2001. The cortical motor system. *Neuron* 31, 889–901.
- Rizzolatti, G., Fadiga, L., Gallese, V., Fogassi, L., 1996. Premotor cortex and recognition of motor actions. *Cogn. Brain Res.* 3, 131–141.
- Rizzolatti, G., Fogassi, L., Gallese, V., 2001. Neurophysiological mechanisms underlying the understanding and imitation of action. *Nat. Rev.* 2, 661–670.
- Rosenbaum, D.A., Meulenbroek, R.J., Vaughan, J., Jansen, C., 2001. Posture-based motion planning: applications to grasping. *Psychol. Rev.* 108, 709–734.
- Schaal, S., Ijspeert, A., Billard, A., 2003. Computational approaches to motor learning by imitation. *Philos. Trans. R. Soc. London, Ser. B* 358, 537–547.
- Umiltà, M.A., Kohler, E., Gallese, V., Fogassi, L., Fadiga, L., Keysers, C., Rizzolatti, G., 2001. I know what you are doing: a neurophysiological study. *Neuron* 31, 155–165.
- van der Meer, A.L.H., van der Weel, F.R., Lee, D.N., 1995. The functional significance of arm movements in neonates. *Science* 267, 693–695.
- Wang, X.J., 2001. Synaptic reverberation underlying mnemonic persistent activity. *Trends Neurosci.* 24 (8), 455–463.
- Wilson, H.R., Cowan, J.D., 1973. A mathematical theory of the functional dynamics of cortical and thalamic nervous tissue. *Kybernetik* 13, 55–80.
- Wohlschäger, A., Gattis, M., Bekkering, H., 2003. Action generation and action perception in imitation: an instantiation of the ideomotor principle. *Philos. Trans. R. Soc. London, Ser. B* 358, 501–515.
- Wolpert, D.M., Doya, K., Kawato, M., 2003. A unifying computational framework for motor control and social interaction. *Philos. Trans. R. Soc. London, Ser. B* 358, 593–602.
- Zhang, K., 1996. Representation of spatial orientation by the intrinsic dynamics of the head direction cell ensemble: a theory. *J. Neurosci.* 16, 2112–2126.